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BOTANICAL GAZETTE

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THE MORPHOLOGY OF ARAUCARIA BRASILIENSIS

I. THE STAMINATE CONE AND MALE GAMETOPHYTE

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(WITH ELEVEN FIGURES AND PLATES IV AND V)

Introduction

Although wood of the araucarian type, strikingly resembling that of the ancient Cordaitales, has been known for a long time and has been used as evidence of the antiquity of the araucarians and as a proof of their relationship to the Cordaitales, both of these opinions have been vigorously challenged. It has been asserted that they are less ancient than the Abietineae and are derived from them (**7, 9**); that possibly they are not related to other gymnosperms at all and have been derived from a lycopod ancestry (**17, 18, 20**); that "the geological claim for the great antiquity of the Abietineae thus fails on critical study of the two forms upon which it is based" (**27**); that "the ancient geological and widely separated geographical distribution (of Araucarineae), the large microsporangiate cones in comparison with the megasporangiate cones, the evident transition between the sporophylls and the foliage leaves are indications of an interesting and probably primitive group. The anatomy of the microsporophylls and megasporophylls indicates that they are homologous structures, functionally differentiated" (**26**); that "unfortunately, no teratological phenomena, on which he always laid great stress, were known in the *Araucariae*, but they were in the Abietineae and showed that the single ovule was a modification of an axillary shoot bearing sporangia" (**30, 31**).

In the face of opinions so diverse, the desirability of additional facts is very evident. We know already that the pollen grains and pollen tubes of *Araucaria* contain numerous nuclei, most of which are prothallial or vegetative (**13, 24, 25, 26**), and that the same condition obtains in *Agathis* (**24**), with the added information that there are definitely "two large male nuclei" (**6**). Among the Podocarpineae the same conditions are known to be true for *Podocarpus* (**1, 2, 5, 8, 22, 33**), *Dacrydium* (**8, 23, 32, 33**), *Phyllocladus* (**11, 33**), *Saxegothaea* (**15, 29**), and *Microcachrys* (**28**). The present investigation was undertaken in the belief that additional knowledge of the morphology of the Araucarineae would aid very materially in clarifying our ideas concerning the origin (or origins) of Coniferales and the relationship of the Pinaceae, particularly the Abietineae, and the Podocarpineae (and Taxaceae generally).

The materials for this investigation have been secured through the kindness of Mr. JAMES C. FLOOD of San Francisco, California, from his country place, Linden Towers, at Menlo Park, California, to whom the writer wishes to express his sense of obligation and appreciation. He is also under obligation for actual assistance in making the collections to the generous assistance of Mr. ROACH, the gardener at Linden Towers, to whom also his thanks are due. Collections were begun in March 1910 and made weekly up to the middle of November, when they were interrupted by illness until February 1911. Collections were again made from November 15, 1911, to February 1912, thus completing the series.

Various killing and fixing agents have been tried. A solution recommended by JUEL (**10**) gave as satisfactory results as any for most stages. Flemming's stronger solution, as well as the chromacetic mixture recommended in CHAMBERLAIN'S *Methods in plant histology*, also gave good results for some stages, but fails to penetrate the microsporangium during the development and division of the mother cells, owing partly to the nearly impervious epidermis that develops about this time, and partly, perhaps, to the presence then in the pollen sacs of a sort of mucilage, apparently produced by the degeneration of the walls of the mother cells. At certain times in mid-winter practically all stages of the cones are present on the trees at the same time. Notwithstanding the fact just mentioned, stages between the prophase of the mother cell and tetrads were collected only four times, though diligently sought for. The same is true of the stages in the development of the gametophyte from mature microspores to those in which the primary spermatogenous cell has already divided. The reasons for this state of affairs are not very apparent, though it may be that these stages are passed through very rapidly or that division occurs during the night.

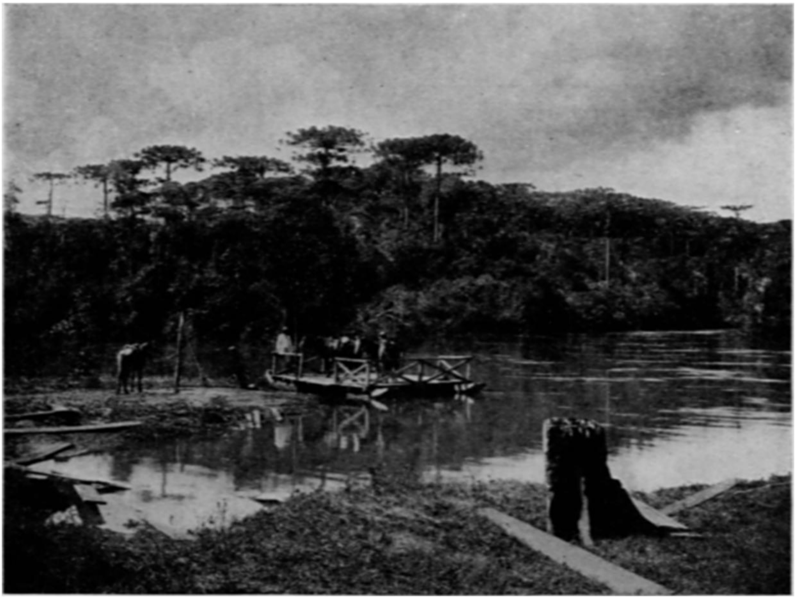


FIG. 1.—Forest of *Araucaria brasiliensis* on the Rio Tibagy, State of Parana, southern Brazil.—Photograph by J. C. BRANNER.

The habit of the tree is shown in text fig. 1, representing old trees in their native habitat, and in text fig. 2, an ovulate tree from the gardens at Linden Towers.

The staminate cone

Among the numerous specimens of *Araucaria* in these gardens, belonging to at least four different species, there are three staminate ones of *A. brasiliensis*. They are about 30 years old and range in height from 25 feet to about 60 feet. The largest one is about 20 inches in diameter. Most of the collections were made from the smallest tree because it has had the crown broken out, and on this account fruits much nearer the ground, a matter of some consequence when one considers ways and means of securing cones from a "monkey puzzle" tree. This tree was selected for the additional reason that the range of stages on it at any time was greater. It had moreover the peculiarity of forming its cones much earlier in the fall and continuing to form new ones later in the

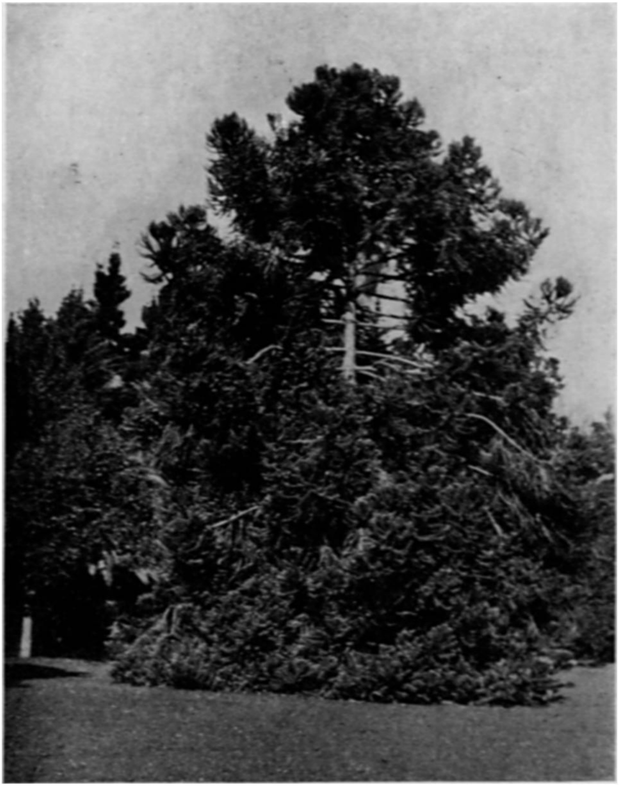


FIG. 2.—Ovulate tree from gardens at Linden Towers, showing retention of lower branches in young trees.

spring. Numerous collections were made from one of the other trees in order to make sure that development in the cones from all the trees was the same.

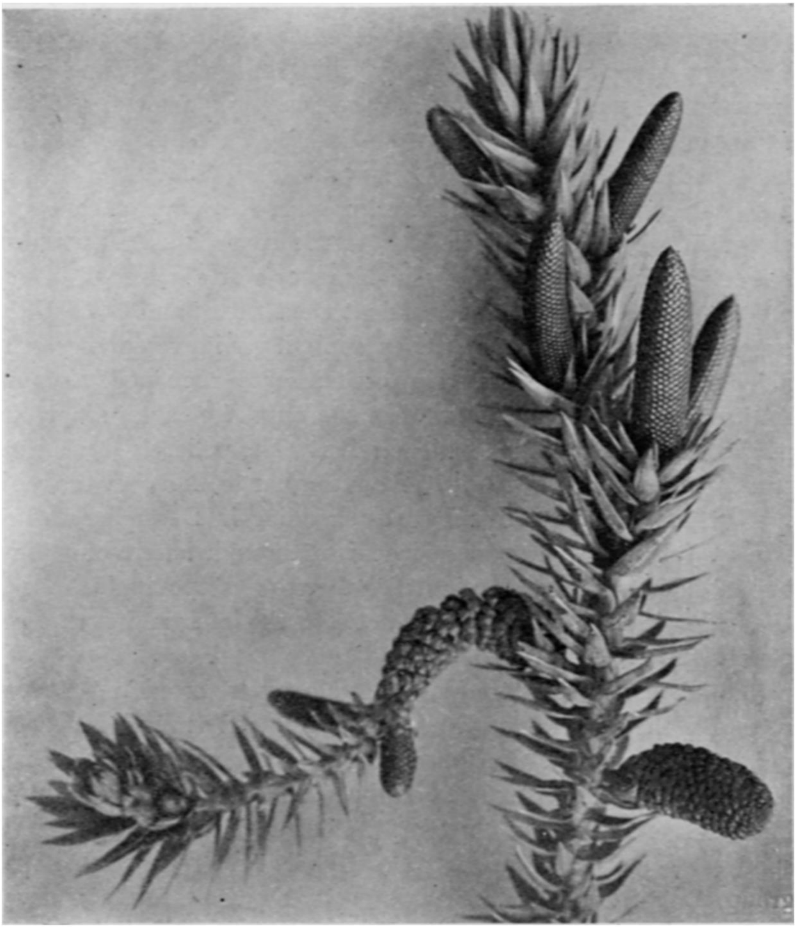


FIG. 3.—Staminate branch of *A. brasiliensis* bearing two old cones of previous season and several young ones; note the new shoot from one of the old cones.

In the fall (August to October) one finds the shoots of *A. brasiliensis* tipped with terminal buds, in some of which, distinguished by being larger and plumper, one can find the very young cones. As soon as the branch has developed from such a bud, one usually finds about 3–6 staminate cones scattered along the new shoot (text fig. 3). Each cone terminates a short leafy branch, which may occasionally continue its growth the following season, but usually the cone dries up, turns brown, and falls off the winter following the shedding of its pollen (text fig. 3). The mature cones are very large, immediately after having shed their pollen being frequently as much as 15 cm. long and 3 cm. in diameter; they are about one-third smaller before shedding. Text fig. 4 shows an unopened cone, a cone shedding its pollen, and the apical view of a mature cone broken in two, about natural size. Such a cone as is shown in the photograph has about 1000 sporophylls, disposed in about 12 spiral rows, each of which makes 2 or 2.5 turns. There are usually 10–15 sporangia, pendent (text figs. 5 and 6) from the expanded distal portion of the sporophyll on its morphologically abaxial side. Each sporangium contains 500–1000 pollen grains. A little calculation will show that the output of a terminal bud may easily reach a billion pollen grains. The pollen is shed in the spring from the first of April to the latter part of May for the most part, although I have found cones shedding in December and as late as July 1. The sporangia dehisce through longitudinal slits on the sides of the sacs facing the other row of sporangia, so that the pollen is shed into the space between the inner and outer rows of sporangia.

By dissecting the terminal buds already referred to, one can recognize the young cones when they are merely rounded growing points. Each one is enveloped in two or three layers of delicate leaves and is slightly flattened on the side next the main axis of the bud. Plate fig. 1 shows a slightly older cone, on which the first sporophylls are forming. A sporophyll is first recognizable as a group of meristematic cells (plate fig. 2) just beneath a slight emergence of the smooth surface of the growing point (plate fig. 1). This emergence increases in size rapidly by growth throughout. Very soon its distal end expands until the whole structure somewhat resembles a mushroom with a very short stalk and one-half of the pileus removed. The stalk is so short that the abaxially placed swollen portion of the sporophyll is in contact with the cone axis. From its surface grow the sporangia, elongating toward the cone

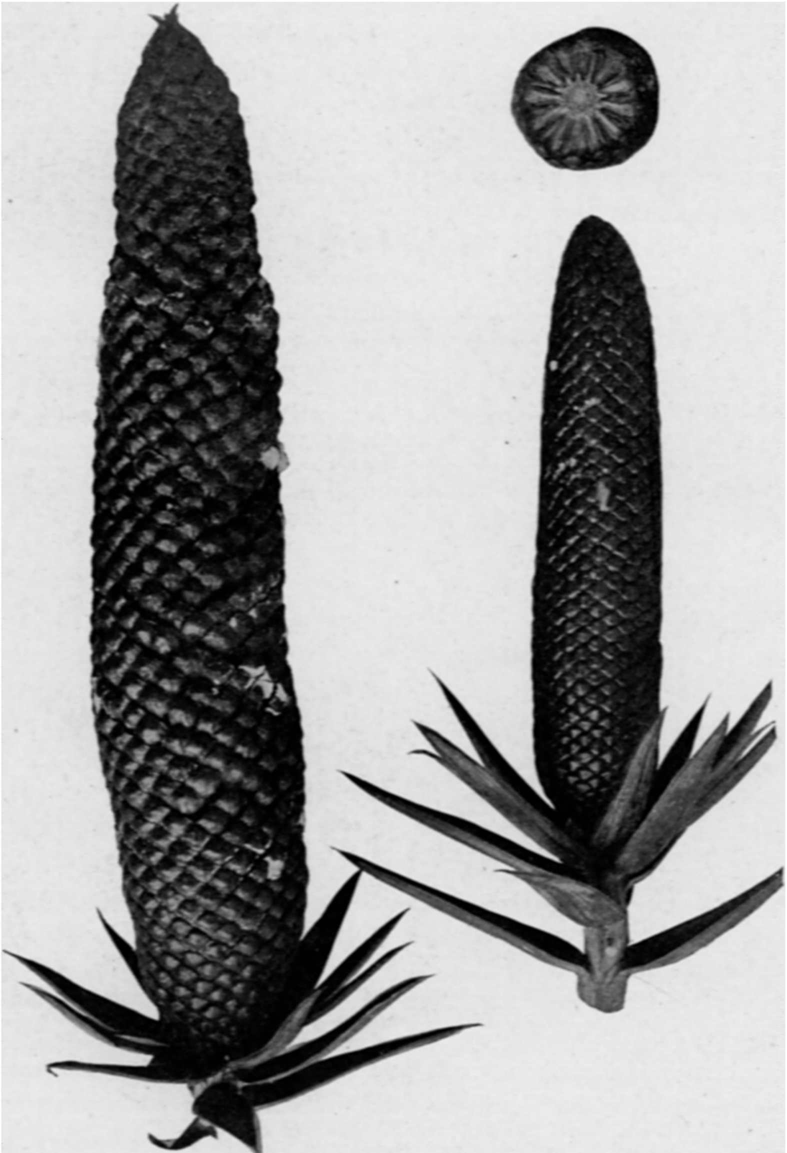
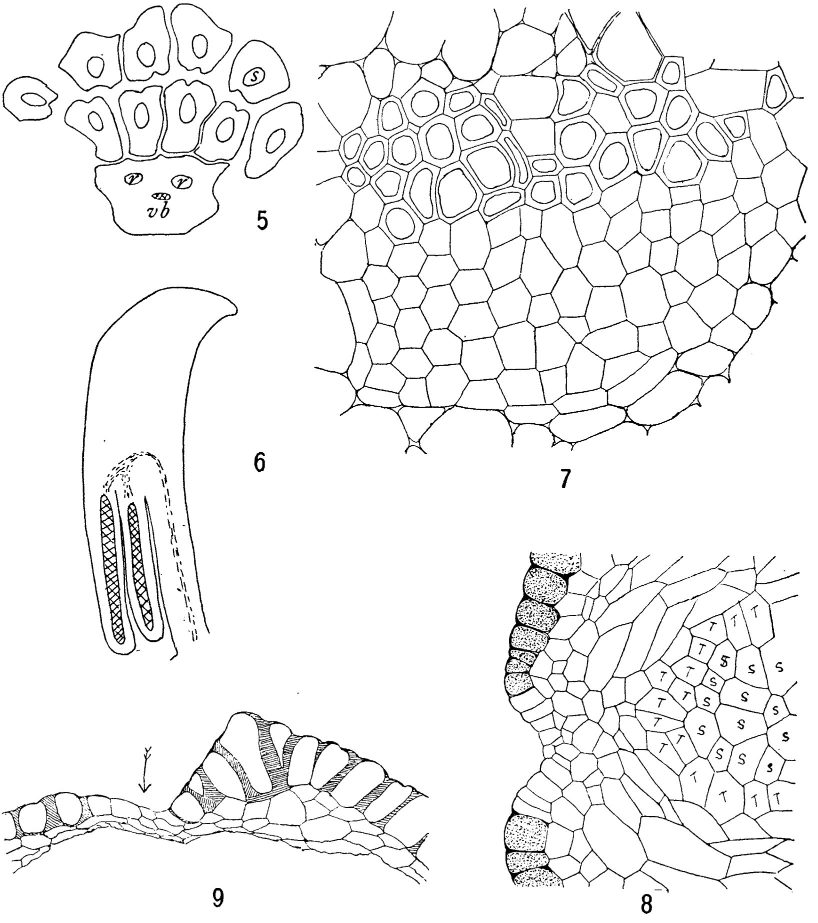


Fig. 4.—Cone shedding pollen (to right), mature unopened cone, and cross-section of mature cone; natural size.

axis as fast as the axis of the sporophyll itself elongates. Like the sporophyll itself, the sporangia are first distinguishable as meristematic outgrowths consisting of several cells. Plate fig. 3 shows part of three sporangia adjacent to one another in the same row, and plate fig. 4 shows a section at right angles to it, showing the



FIGS. 5–9.—Fig. 5, cross-section of sporophyll, showing relation of sporangia to one another and to the stalk; fig. 6, longitudinal section of a sporophyll, showing position of sporangia and course of their vascular supply; fig. 7, cross-section of a vascular bundle of sporophyll; fig. 8, cross-section of a sporangium at mother cell stage, showing sporogenous cells (*s*), tapetal cells (*t*), 4–6 layers of wall cells, tannin-filled epidermal cells, and thin cells where dehiscence will take place; ×250.; fig. 9, annulus and stomium just before dehiscence; ×250.

beginnings of two sporangia adjacent to one another but in different rows.

Occasionally one can distinguish what appears to be the archesporium almost as soon as the sporangium itself is recognizable, but much more commonly it cannot be detected until the sporangium is 12–15 cells in length and 8–10 cells wide (plate figs. 4, 5, 6). Not infrequently sporangia as far developed as that shown in plate fig. 7 do not show any differentiation of sporogenous cells. Ordinarily one can recognize all the primary regions of the sporangium at this stage. The cells of the tapetum seem to be derived more or less indifferently from those of the wall layers outside, or from derivatives of the inner and presumably sporogenous cells. However, I should not like to be too dogmatic in regard to this. Multiplication of cells continues until the sporogenous tissue consists of a mass some 20 cells in cross-section (plate fig. 8) and 40–50 cells long. The tapetum remains one or two cells thick, the ultimate cells being elongated radially and retaining their position and structure till some time during the development of the male gametophyte. At this time there are 4–6 layers of wall cells radially flattened, with very little cell contents. The epidermis is at this time filled with a densely staining substance, resembling tannin in its staining reactions, and presenting a very effective barrier to the ready penetration of the ordinary reagents. In the further development of the sporangium the contents of these epidermal cells disappear, and the radial walls, seen in a cross-section of a sporangium, thicken in the fashion of a fern annulus, except at the point of future dehiscence. The wall cells are eventually crushed and more or less destroyed and the tapetum finally disintegrates (text figs. 8 and 9).

Sporogenesis

After the last division of the sporogenous cells, the mother cells begin enlarging, until at the prophase of the heterotypic division they have attained a diameter more than twice that of the sporogenous cells. This eight or ten times increase of volume is largely water, the cytoplasm becoming greatly vacuolated as the growth increases. There is a corresponding enlargement of the nucleus, though not proportionally so great (plate fig. 9). Once this increase in size has been effected in the mother cells and their walls, the cell contents appear to round up and shrink away from the walls more or less; just how much I am unable to say owing to the difficulty of determining whether part or all of the shrinkage may not be due to the difficulties of securing satisfactory fixation. The walls themselves have a tendency to persist until after the young spores have been formed, but apparently they change their chemical condition and become more or less mucilaginous in character. Sometimes no walls at all are visible, but the spaces among the mother cells are filled with a thin sort of mucilage. The greater the amount of this mucilage present, the poorer the fixation.

Owing to the difficulties already mentioned, I have but little trustworthy information concerning the course of events during the reduction divisions. Stages in the formation of the presynaptic spireme, synapsis, and diakinesis were observed. At the metaphase of the heterotypic division there are 8 bivalent chromosomes, but the material did not permit one to follow the method of their formation. The spindle fibers are attached to their apices (plate fig. 11), and they are drawn apart as short stubby masses and collect at the pole in a close mass. They appear at the spindle of the homeotypic division as much longer rods curved into more or less U-shaped chromosomes. No walls are formed, apparently, until after the spore nuclei have passed into the resting condition, when a system of fibers is present between the nuclei, on which the plasmatic membranes separating the young spores arise (plate figs. 13 and 14).

The young spores now form walls around themselves, entirely within the old mother cell wall if it is still present. The spores then begin a slow enlargement and thickening of the walls. At first the growth consists merely in enlargement of the wall without any apparent increase of cytoplasm or nucleus. There is either one very large vacuole almost entirely filling the spore or many smaller ones separated by only the most tenuous cytoplasmic walls. At this time no inclusions of starch or other food materials are visible. After the spore wall has reached its mature size, but not final thickness, the cytoplasm becomes more abundant and the nucleus enlarges (plate figs. 16 and 17). In the large nucleus there is a large nucleolus and rather scanty chromatin. From this is organized a rather long, loose spireme, apparently containing scanty chromatin. It segments to form 8 chromosomes, which contract into rather small dense oval masses (plate fig. 18).

Male gametophyte

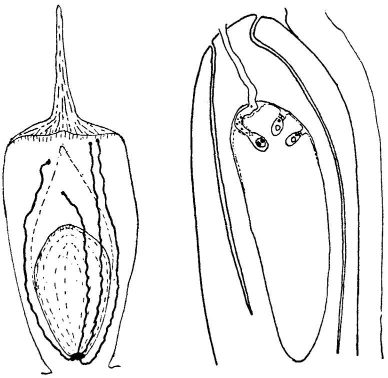
The results of this first division are a primary prothallial cell and a free nucleus (plate fig. 19). The latter at once divides to produce a second prothallial cell, which takes its place over the preceding. The next division yields the free tube nucleus and the primary spermatogenous cell (plate fig. 21). Meantime the prothallial cells have divided (plate figs. 20, 21, 22). The primary spermatogenous cell now divides, yielding the usual stalk and body cell. The stalk cell is very evanescent, usually becoming confused with the general cytoplasm very quickly. Plate fig. 25 shows one of the few preparations in which it could still be distinguished as a distinct cell. Another interesting case was observed in which there seemed to be two free and equal cells in the unshed pollen grain. The usual condition of a mature pollen grain, with 15–25 free prothallial nuclei, a recognizable tube nucleus, and a single body cell, is shown in plate fig. 27.

It is in this condition that the pollen is shed in April (usually). The potential number of pollen grains is four to eight times as great as the actual number formed. It has already been remarked that the ordinary number of mother cells is about 1000, while the usual number of pollen grains that mature in a sporangium is only 500–1000. At the time they are shed the pollen grains have a two-layered wall, the outer coat of which easily separates from the inner (plate figs. 25, 26, 27), but which does not appear to do so naturally to form wings. At the time they are shed they contain a great many very large starch grains, a few of which are shown in plate fig. 27. They are usually so crowded with it that the microtome knife scatters the contents all about in cutting sections of shed pollen.

Pollination

The ovulate cones are first recognizable in late April. At this time there is no trace of ovules on the scales and the pollen lodges somewhere near the free edge of the so-called ligule (text fig. 10).

Whether the pollen shed in the early part of the season finds a lodgment in a position to become effective is uncertain. Neither does there appear to be any available data as to whether this precocious shedding of pollen occurs in its native habitat. Though California and Brazil exhibit a somewhat rough correspondence in their seasons of rainfall and plant growth, yet it is probably not sufficiently exact to permit of any very satisfactory inferences as to the corresponding behavior in the two habitats.



FIGS. 10, 11—Fig. 10, ovule and scale in December, showing course of pollen tubes; fig. 11, course of pollen tube through nucellus to archegonium.

I have not yet ascertained certainly how long a time elapses after the pollen falls on the scale before germination occurs. Grains that have germinated can be found in the latter part of summer after the fogs have set in. Meantime during the summer the ovule is forming and the stigmatic nucellus is usually ready to receive the advancing pollen tubes some time in September or October.

I have not so far succeeded in germinating pollen to any very advanced stage, nor have I been able to follow with any certainty the course of events in the pollen tube before it reaches the nucellus. When the ovuliferous scales are pulled apart, very numerous pollen tubes are usually found sewed back and forth between the two adjacent surfaces of the scales. One can sometimes isolate one without completely destroying it, but I have learned from such preparations nothing more than that there are numerous nuclei and a body cell present. One could infer that they would be there, inasmuch as they were in the pollen grain, and they are afterward present in the tube when it enters the nucellus. Whether division of the prothallial nuclei occurs in the tube or not is uncertain, owing to the fact that I have never been able to obtain an entire tube in which I could count the nuclei and be sure of having seen them all. These nuclei do increase markedly in size, and much of the starch which entered the tube at germination disappears before penetration of the tube into the nucellus.

At the time that the tube enters the nucellus there are numerous nuclei and the body cell present. I was unable to distinguish the tube nucleus any longer from the others. At first only a few of these nuclei enter the portion of the tube in the nucellus. The body cell is usually in that portion just outside of the nucellus or just barely within it. There is apparently very little activity in the development of the tube from the time it first penetrates the nucellus for a short distance until spring. I did not succeed in finding the mitosis concerned in the division of the body cell, though the two male cells were found two or three times still imbedded in a common mass of dense cytoplasm. The two nuclei frequently differ in size markedly. The body cell and its nucleus have increased in volume after leaving the pollen grain some six or eight times by the time the pollen tube has penetrated the nucellus in October (plate fig. 28). This increase continues on an even greater scale up to the time of division. After the division of the body cell, one, at least, of the pieces organizes itself into a large male cell or perhaps a real sperm. These vary considerably in size and in the definiteness of their organization. They all agree in being very large and in being more or less completely delimited from the cytoplasm in which they are imbedded (plate fig. 29). Almost invariably the large nucleus is at the extreme end of the cytoplasm and the cytoplasm is very often evidently arranged in such a way as to lead one to surmise that the nucleus actively changes its position in reference to the cytoplasm. The nucleus is invariably at that extremity which would lead in the direction that the "sperm" would be inferred to be moving. The cytoplasmic body is sometimes bent, almost at a right angle in one instance observed, in such a way as to remind one strongly of the creeping movements of an amoeba. In one instance of two "sperms" lying in a common mass of cytoplasm, apparently having just divided, there was present a peculiar fibrillar structure reminding one of a nuclear spindle without the chromosomes and with an aster at either pole. Whether this is an indication of the presence of a blepharoplast and whether the "sperm" is actually motile, I hope to be able to ascertain during the coming spring. The division probably occurs in the latter part of February and in the part of the tube outside of the nucellus.

During this time the pollen tube has advanced through the nucellar tissues in a more or less irregular and branching course. When it reaches the upper part of the female gametophyte it usually turns aside from the apex, which is protected by a cap of crushed nucellar cells, and creeps laterally along the surface of the gametophyte until it reaches the narrow opening leading down to one of the archegonia, down which it descends to the neck of the archegonium. Here it becomes perforated. The "sperm" passes through the opening and crowds the neck cells of the archegonium apart without destroying them, and plunges down into the egg so vigorously as to leave a very distinct wake behind it in the cytoplasm. Fertilization occurs in the latter part of March or first week or two of April.

Discussion

It is not proposed at this time to enter into any general discussion regarding the broader questions that prompted the investigation, but to let that await the issue of further investigation of other phases of the life history of this species and of the other three species of which material is available. However, it may not be amiss to point out that this added information concerning the male gametophyte goes far toward inducing a belief in the primitive condition of the araucarians. It certainly strengthens the resemblance to the podocarps and tends to increase our confidence in their genetic connection. Barring the abnormally large "sperms" of *Araucaria* and the greater number of prothallial nuclei, its male gametophyte exhibits an almost identical structure even in small details with that of the Podocarpineae. On the contrary, it is clear that the type of male gametophyte found in these two tribes is essentially different from that found in *Cupressus Goveniana* (**10**) and *Juniperus communis* (**14**). In these we have a multiplication of spermatogenous cells, which may be induced, as has been suggested, by the opportunity for more than one sperm to function, but in any case is doubtless a reversion to an ancient habit (**10, 14**). This view is strengthened by the occurrence of more than two sperms in *Microcycas* (**3**) and *Ceratozamia* (**4**). The deposition of the pollen at a distance from the nucellus has also been recorded for *Saxegothaea conspicua* (**15**), and serves to strengthen the likeness of the araucarians and podocarps.

By long odds the most interesting and suggestive feature of the male gametophyte of the araucarians yet known is the remarkably large "sperms" and the possibility of their motility. The one figured (plate fig. 29) is about 150 μ long. It is by no means the largest one observed, but seemed to be the one most definitely organized. Such dimensions are only known elsewhere among the actively swimming sperms of the Cycadales and *Gingko*. It is of interest to note that the kauri (**6**) appears to have two large nuclei also, though it is not stated that they constitute part of organized cells. Inasmuch as *Agathis* has usually been held to be more primitive in most respects than *Araucaria*, it may be possible that they will yet be found there. The aster-like fibers found in the dividing body cell are of course very suggestive of a blepharoplast, and one might perhaps legitimately expect such structures to be found in connection with such large and possibly motile male cells. Again they might be only such structures as have been recorded by LAND (**12**) in the egg of *Ephedra*.

Summary

1. The staminate cones are extraordinarily large and have numerous sporophylls with an indefinite number of pollen sacs pendent from the abaxial side of the swollen apex.
2. An almost incomprehensibly great number of pollen grains is produced.
3. The method of differentiating the sporogenous tissue is variable and indefinite. The size of the sporangium and the number of microspores is subject to wide fluctuations.
4. The structures concerned in dehiscence are very fernlike.
5. The chromosome number in the male gametophyte is 8.
6. Prothallial tissue is formed in a manner almost identical with that in the Podocarpineae, but the number of cells so formed is greater.

7. The pollen is shed with numerous prothallial nuclei, stalk nucleus, tube nucleus, and body cell free in it.

8. The pollen does not fall upon the nucellus but upon the ovuliferous scale at a considerable distance from the position of the ovule.

9. About a year elapses between pollination and fertilization.

10. No ovule has yet been formed on the scale at the time of pollination and the pollen tube does not reach the ovule for 5 or 6 months afterward.

11. The body cell is single, at least usually, and large.

12. Two male cells (sperms perhaps) · are formed and are usually unequal.

13. There may be a blepharoplast-like body associated with the division of the body cell.

14. Fertilization occurs about the first of April.

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EXPLANATION OF PLATES IV AND V

All figures have been drawn under Zeiss apochromatic objectives and compensating oculars with the aid of a camera lucida. Figs. 2–8 were drawn with 4 mm. obj. and compensating ocular 6; figs. 9–27, under obj. 3 mm. and ocular 12; figs. 28 and 29, under 3 mm. obj. and compensating ocular 6.

Fig. 1.—Longitudinal section of a young cone from a terminal bud: *sc*, scale leaf; *sp*, young sporophyll; *vb*, vascular bundle; ×12.

FIG. 2.—Primordial meristem of very young sporophyll drawn from same cone as fig. 1; ×250.

FIG. 3.—Cross-section of a cone showing the sporangial meristems; ×250.

FIG. 4.—Longitudinal section of cone of same age as preceding: section passes through the stalk of the sporophyll and through the primordia of one sporangium in each row; *c.ax*, axis of cone; ×250.

FIG. 5.—Transverse section of cone and longitudinal section of sporangium: sporogenous tissue not defined; ×250.

FIG. 6.—Same as fig. 5, but showing usual differentiation of sporogenous tissue (*spt*); ×250.

FIG. 7.—Usual stage of differentiation of tapetum (*t*); ×250.

FIG. 8.—Cross-section of sporangium after last sporogenous division; ×250.

FIG. 9.—Somewhat shrunken mother cell showing eight times increase in volume; ×770.

FIG. 10.—Portion of a nucleus in which the heterotypic chromosomes are forming; ×770.

FIG. 11.—The 8 heterotypic chromosomes; ×770.

FIG. 12.—Second division of mother cell; ×770.

FIGS. 13 and 14.—Tetrads, showing cell division; ×770.

FIG. 15.—A group of young microspores; ×770.

FIGS. 16 and 17.—Mature microspores; ×770.

FIG. 18.—Division of microspore nucleus; ×770.

FIG. 19.—Showing first prothallial cell (*pc'*); ×770.

FIG. 20.—Mitosis of a prothallial cell; ×770.

FIG. 21.—Showing two tiers of prothallial cells (*pc' pc''*), primary spermatogenous cell (*p.s.c.*), and tube nucleus (*t*); ×770.

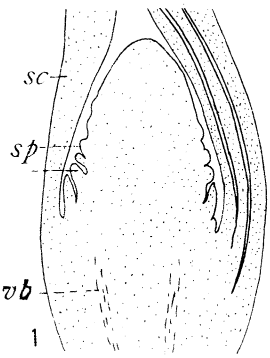
FIG. 22.—Division of primary spermatogenous cell; ×770.

FIGS. 23–26.—Series of transverse sections of a pollen grain: *pc'*, basal tier of prothallial cells; *pc''*, second tier; *tn*, tube nucleus; *bcn*, body cell nucleus; *bc*, body cell; *sc*, stalk cell; *scn*, stalk cell nucleus; ×770.

FIG. 27.—Shedding stage of pollen grain; ×770.

FIG. 28.—Body cell about October 15; ×385.

FIG. 29.—A male cell just before fertilization; ×385.



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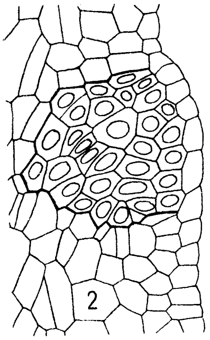

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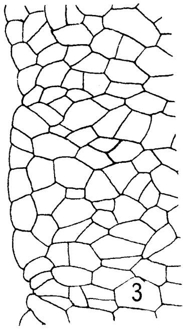

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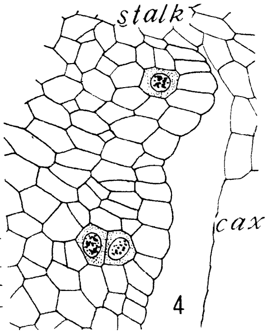

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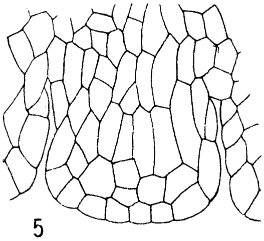

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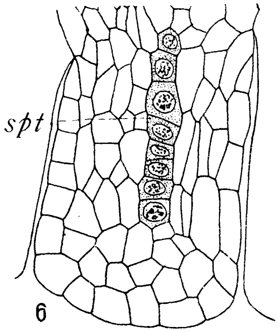

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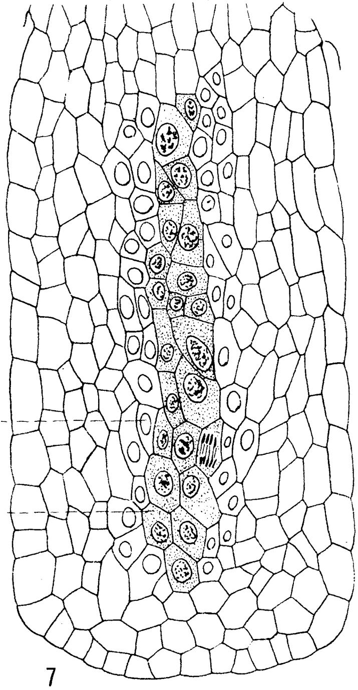

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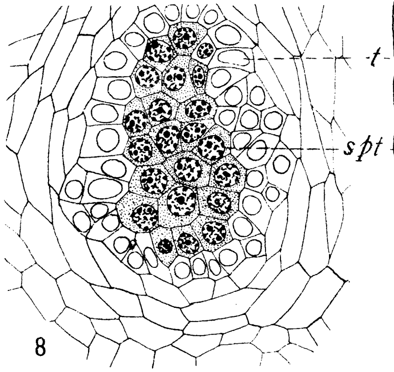

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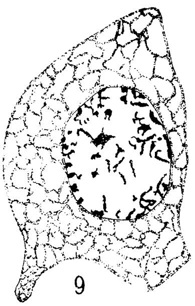

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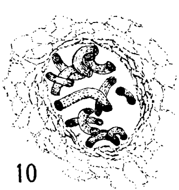

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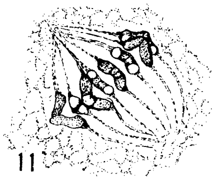

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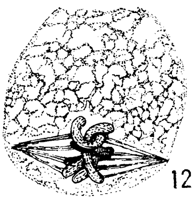

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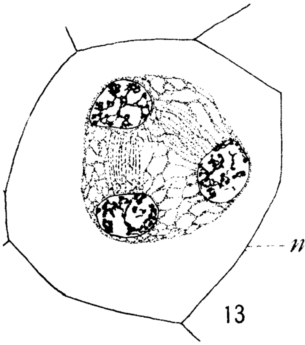

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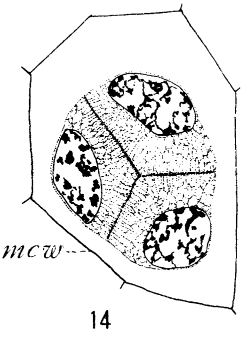

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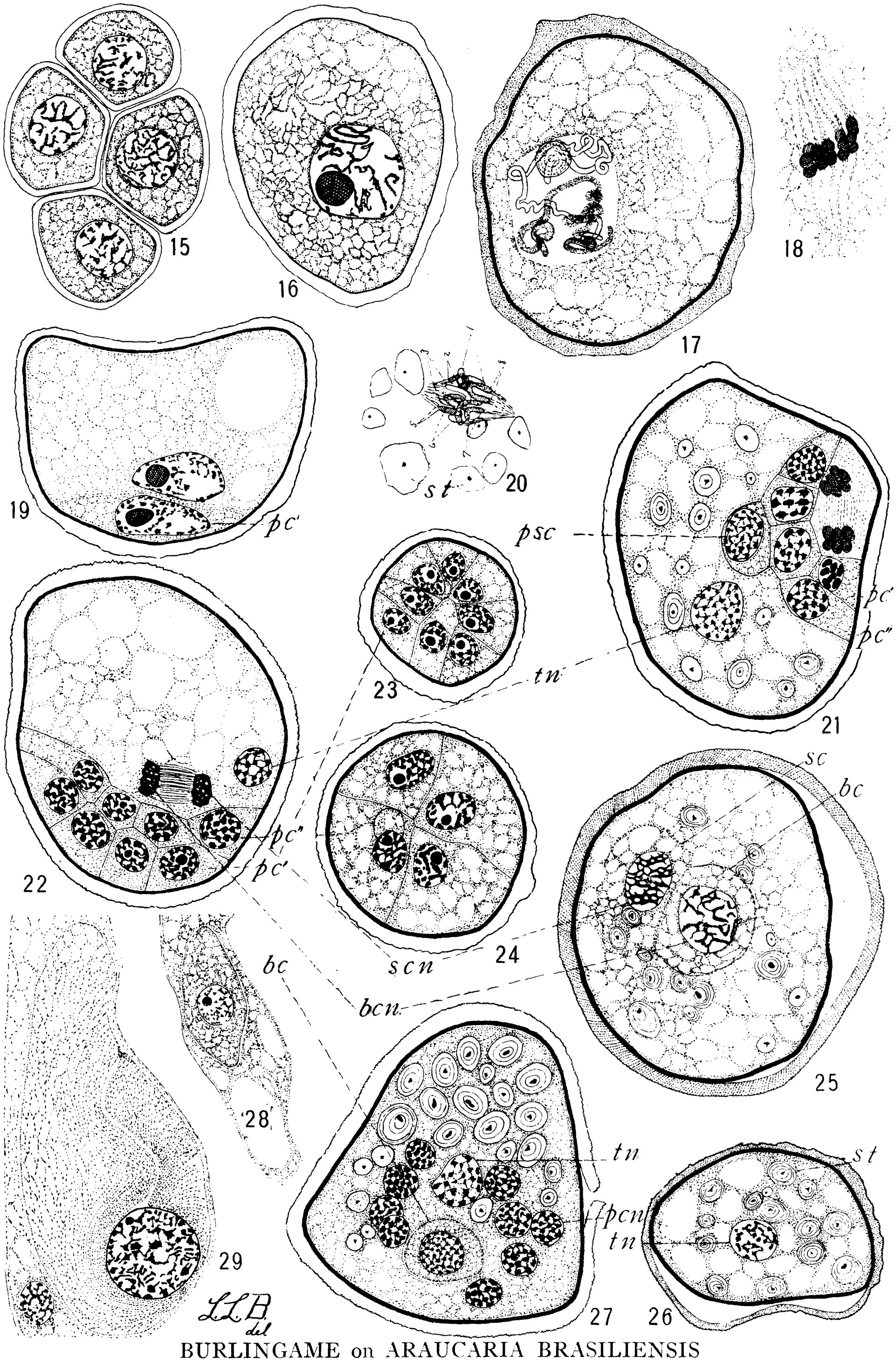

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